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AN ENDOCOCHLUS HAVING BINARY HELICOID THALLI OF LEFT-HANDED ROTATION

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(WITH 6 FIGURES)

Several maizemeal-agar plate cultures which after having been overgrown with mycelium of *Pythium mamillatum* Meurs had been further planted on January 3, 1947, with small quantities of leaf mold kindly collected by Dr. E. B. Toole in an oak wood near Greensboro, North Carolina, in December, 1946, showed, on microscopical examination twenty-seven days later, sparse stands of erect beaked conidia arising in scattered areas from prostrate hyphae often arranged more or less radially. The general aspect of the conidial apparatus indicated clearly a species of *Endocochlus*. While the robust stature of the erect spores was rather strongly suggestive of my *E. gigas* (**6**: 368–371), their longer and accordingly much more conspicuous empty apical beaks made for an appearance alien to that species as well as to the smaller congeneric forms I have described under the binomials *E. asteroides* (**5**: 8–15) and *E. brachysporus* (**6**: 364–367). Closer examination, in which attention was given also to the vegetative and the sexual reproductive stages associated with the conidial apparatus, brought to light morphological peculiarities amply distinguishing the fungus here concerned as a new member of the genus.

Like the congeneric forms previously described, the new species subsists through parasitism on a relatively large terricolous *Amoeba*. Animals in the earlier stages of attack (FIG. 1, *A*; FIG. 2, *A*; FIG. 3, *A*; FIG. 4, *A*) were commonly found to measure from 100 to 130 μ in width when drawn into a rounded shape. They

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were enveloped individually by a firm pellicle that for the most part was cast into broadly undulating folds. Their hyaline, obscurely granular protoplasm surrounded a single prolate ellipsoidal nucleus (FIG. 1, *A, n;* FIG. 2, *A, n;* FIG. 3, *A, n;* FIG. 4, *A, n*), commonly 27 to 32 μ long and 18 to 21 μ wide, that contained at its periphery a large number of globose bodies about 1 μ in diameter. At the two poles of the nucleus these bodies, presumably consisting of chromatin material, were massed several layers deep, while in the equatorial region they were present usually in a single layer. Owing to the deeper accumulation of globose bodies at the poles the homogeneous central portion of the nucleus was often approximately equal in length and width. Many infected animals, as also many healthy individuals of the same species, contained one or more specimens of the testaceous rhizopod *Euglypha levis* (Ehrenb.) Perty (FIG. 1, *A, w;* FIG. 2, *A, w*), which, being abundant in the cultures, had apparently been ingested to serve as food material.

Because of close resemblances in nuclear organization, the protozoan here in question is held referable to *Amoeba papyracea* Penard (8: 201). While the measurements given by Penard for width of rounded individuals—minimum 176 μ, maximum 198 μ—are considerably in excess of those prevailing in my cultures, smaller dimensions would seem to be more or less normal in *Amoeba* populations developing on agar substrata. Previous to its appearance as the animal host of the new *Endocochlus* the protozoan had not been noted in the many agar plate cultures prepared from leaf mold from different sources over a period of more than ten years. Whether its failure to develop more often in plate cultures is due to limited distribution or to special requirements for multiplication, its absence in any material naturally precludes development of the zoöpagaceous form habitually subsisting on it.

Encounter between specimens of *Amoeba papyracea* and the fungus takes place much as in the several other species of *Endocochlus* made known earlier. When the *Amoeba* in its ordinary locomotion comes in contact with a conidium of the parasite the conidium remains affixed to the animal's pellicle, apparently through adhesion. From the adhering region the spore soon puts forth a bulbous protuberance, about 3 or 4 μ wide, which serves presumably as an appressorium since its rather thick wall usually shows later the yellowish coloration characteristic of adhesive structures in the Zoöpagaceae. The protuberance soon begins to elongate apically as a germ tube, in many instances at first pushing the pellicle inward to form a funnel-shaped depression. After the pellicle has been ruptured under increasing pressure the germ tube continues its growth some little distance into the protoplasmic interior. Elongation then ceases, and the narrowed tip of the germ tube abruptly begins expanding into a bulbous swelling (FIG. 1, *A, a*). Through progressive vacuolization the contents of the adhering conidium migrate gradually into the terminal swelling. When this migration is completed the externally adhering conidial envelope is wholly empty, as is also the germ tube on whose tip is then borne a prolate ellipsoidal or nuciform cell (FIG. 1, *A, b*) densely filled with protoplasm. Disturbances deriving from the movements of the animal readily suffice to detach the nuciform cell from its slender support. Following such disjunction the empty germ tube together with the conidial envelope is shed by the animal; while simultaneously the nuciform cell, or infective body (FIG. 1, *A, c*), immersed in its mobile protoplasmic ambient, begins autonomous parasitic development.

With the assimilation of nourishment from the host protoplasm, the infective body here sometimes grows out nearly as in the other known species of *Endocochlus,* by putting forth from its distal end a single prolongation that usually begins curving at an early stage (FIG. 1, *A, d, e;* FIG. 2, *A, a;* FIG. 3, *A, a-c*) to form a close helical coil (FIG. 1, *A, f;* FIG. 3, *A, d, e*), which, after describing one and one-half to two turns, may branch dichotomously (FIG. 3, *A, f, g*). Even where only a single thallodic coil is formed the present fungus shows for some time, if not to the end, a distinctive peculiarity in that the prolongation is, as a rule, at least in its proximal portion, conspicuously narrower than the infective body, so that this body stands out as a proximal swelling. In contrast, the infective bodies of congeneric species, and also of those species of *Cochlonema* having a similar manner of invasion, grow out distally at an increasing width and thus become merged indistinguishably with the resulting thallus.

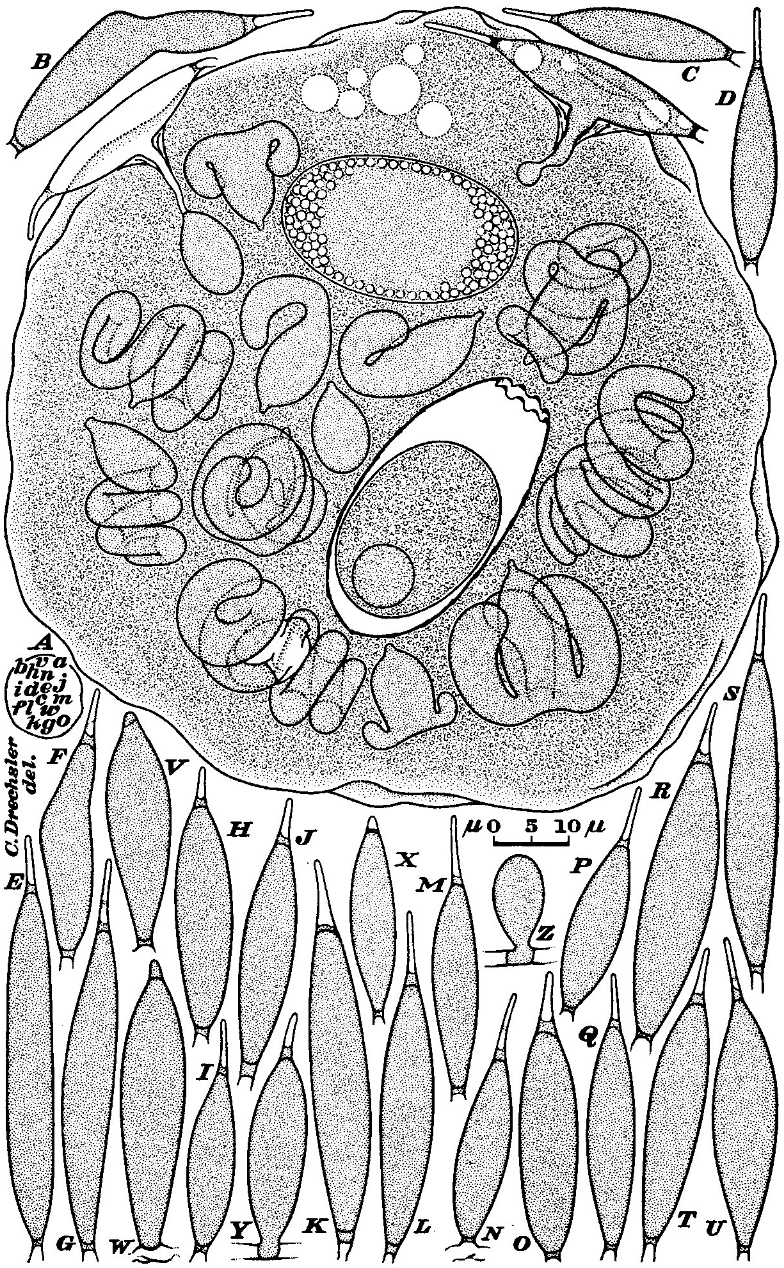

FIG. 1. *Endocochlus binarius.*

Although the production of a single thallodic coil is hardly infrequent in the present fungus, the much more usual manner of development here is by the extension of two thallodic coils. The two coils arise as small buds from opposite sides at the distal end of the infective body (FIG. 1, *A, g*). Through continued elongation, together usually with some distal widening and with constantly winding curvature (FIG. 1, *A, h*), they develop, as a rule, on opposite sides of the infective body, into helical coils which commonly remain unbranched until they have described one and one-half to two turns (FIG. 1, *A, i-l;* FIG. 2, *A, b-h;* FIG. 3, *A, h, i;* FIG. 4, *A, a, b*). Somewhat contrary to expectations that might be entertained, the coils are not oriented usually with their axes extending away directly from the sides of the infective body to which, respectively, they are attached, but instead are oriented with their axes perpendicular to the plane passing lengthwise through the middle of the infective cell and bisecting the basal attachments of both coils. The considerable measure of uniformity in positional relationships of the binary thallodic coils—a measure of uniformity seeming all the more remarkable because it is achieved despite constant disturbance from promiscuous movement of the protoplasmic ambient—is to be attributed to unusually consistent directive tendencies in growth that become manifest early in the elongation of the buds. After the initial abrupt curvature of the buds toward the proximal end of the infective body (FIG. 1, *A, g*), further curvature is such that if the infective body lies with its longitudinal axis in the plane of the microscopical field and with its proximal end directed toward the observer, the bud arising from the right side of the distal end will elongate with its advancing tip interposed between the observer and the infective body, while the bud from the left side of the distal end will elongate with its advancing tip passing underneath the infective body into partial concealment from the observer (FIG. 1, *A, h*). The three-dimensional curvature thus initiated is continued with further growth of the two buds; so that with the infective body oriented in the way just described, the bud arising on the right side of the distal end is soon found prolonged into a helical coil overlying the infective body and with its axis directed toward the observer in a line nearly parallel with his line of vision, while the bud arising from the left side of the distal end

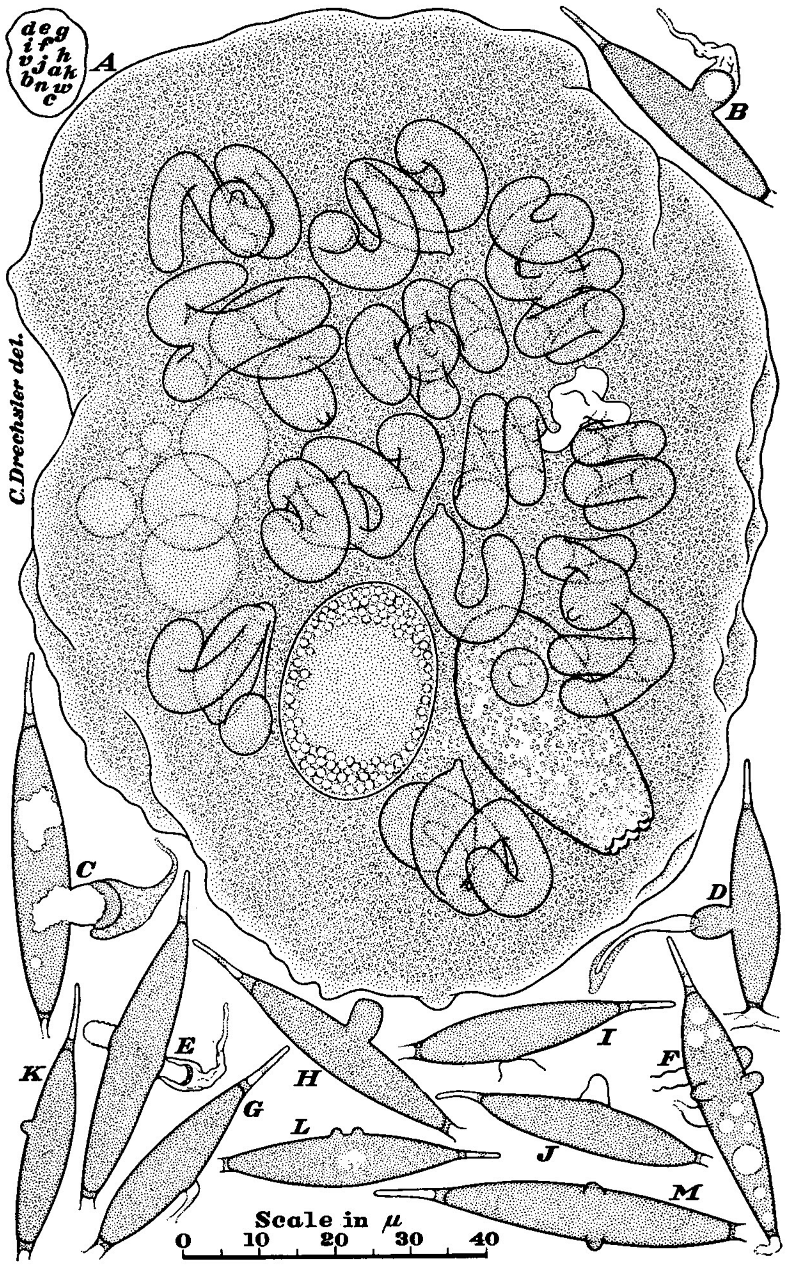

FIG. 2. *Endocochlus binarius.*

will be found extended into a similar coil underneath the infective body and with its axis directed vertically downward in a line likewise approximately parallel to the line of vision (FIG. 1, *A, l;* FIG. 3, *A, h;* FIG. 4, *A, b*). Curvature in similar relationship to the infective body and in the same direction of rotation prevails also where only one thallodic coil is produced, as well as in the occasional instances where three coils are formed (FIG. 1, *A, o*). Thus, regardless of variation in number, the coils consistently show rotation of the same direction as is found in the threads of a left-handed screw. To cite familiar examples from phanerogamic plants, the rotation shown here corresponds to that displayed in the twining stems of the common hop, *Humulus lupulus* L., and the black bindweed, *Polygonum convolvulus* L. Among fungi similar left-handed rotation occurs as a distinctive feature in the helicoid ascospores of my *Cochliobolus heterostrophus* (**2**, **4**), in the conidia of my *Harposporium helicoides* (**7**), in the coiled sporogenous tips of the sporophores of my *Helicocephalum oligosporum* (**3**), as well as in the aerial sporogenous branches and spore chains of some helicoid species of *Streptomyces* (= *Actinomyces*) as, for example, *S. lavendulae* (Waksm. & Curt.) Waksm. & Henr. (**1**: 150–151; **9**; **10**: 944).

Since both of the two thallodic coils usually produced show rotation in the same direction they could well be regarded, especially during their earlier stages of growth, as making up a single binary helicoid structure modified midway between the ends by the presence of the protuberant infective cell. In many instances, however, the continuity of the combined structure is interrupted through evacuation of the infective body together usually with a proximal portion of the thallodic coils (FIG. 1, *A, k;* FIG. 2, *A, h;* FIG. 4, *A, a*); the larger, living portion of each coil then becoming delimited proximally by a retaining wall. The empty envelopes of infective bodies, after some time, often vanish completely from sight; so that, eventually, many of the larger thallodic coils (FIG. 3, *A, j;* FIG. 4, *A, c*) come to appear little different, at the proximal end, from those of other species of *Endocochlus,* where the infective body, because of its broad elongation from the full width of its distal end, merges indistinguishably with the thallus.

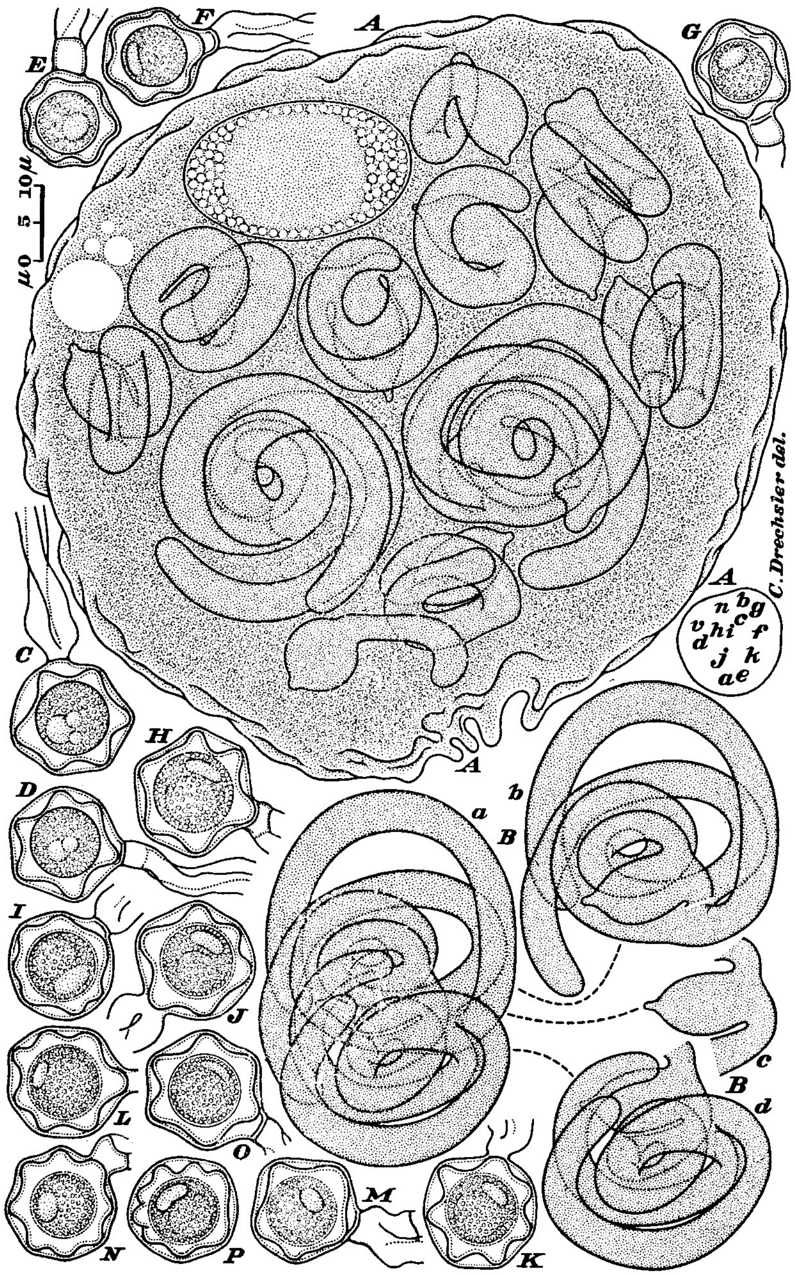

FIG. 3. *Endocochlus binarius.*

The larger thallodic coils are branched in varying measure, as many as three successive bifurcations often being recognizable (FIG. 4, *A, d*). Whether a coil is of solitary (FIG. 2, *A, i;* FIG. 3, *A, f, g*) or of twinned (FIG. 1, *A, m.* FIG. 3, *A, j, k; B, a-d.* FIG. 4, *A, c, d*) origin, its first dichotomy usually takes place after one and one-half to two turns have been formed, though thalli are not rare wherein much earlier bifurcation is clearly evident (FIG. 2, *A, j, k*). Following the first dichotomy, elongation of the branches is marked by diminished curvature, with the result that a thallodic coil whose first two turns may have an outer diameter equal to the length of the parent infective cell will after three successive dichotomies extend its eight branches rangily over an orbit three or four times wider (FIG. 4, *A, d*). Owing apparently to their rather open arrangement the longer terminal elements of well developed thalli are somewhat readily displaced from their original positions when they are jostled by other thalli in an animal under multiple attack. Accordingly in later stages of infection the larger thalli lose much of their geometrical symmetry as they are pressed together closer and closer. Before the protozoan host is incapacitated for further movement, primarily from advanced depletion of its protoplasm, the several thalli become confusedly intertangled in a dense clew (FIG. 5, *A, B*).

Although for a time after its disablement the infected specimen of *Amoeba papyracea* continues to operate its contractile vacuole (FIG. 5, *A, v; B, v*), further expropriation of its protoplasm and progressive degeneration of its nucleus (FIG. 5, *A, n; B, n*) eventually leads to the extinction of all signs of life. At this stage, or frequently a little earlier, the several thalli begin reproductive development. Where an infective cell is still present it often serves directly in putting forth one (FIG. 6, *A, a*) or more (FIG. 6, *B, a, b*) reproductive hyphae, while others are being extended from proximal positions on the associated coil (FIG. 6, *A, b*) or coils (FIG. 6, *B, c, d*). Naturally in those instances where the infective cell has been lost, all reproductive hyphae (FIG. 6, *C, a-h*) arise from the thallus, and in some instances all reproductive hyphae (FIG. 6, *D, a-g*) originate from the thallodic coils even where the infective body remains intact. The growth of the reproductive hyphae (FIG. 6, *E, a-d*) is accompanied by vacuolization and evacuation of

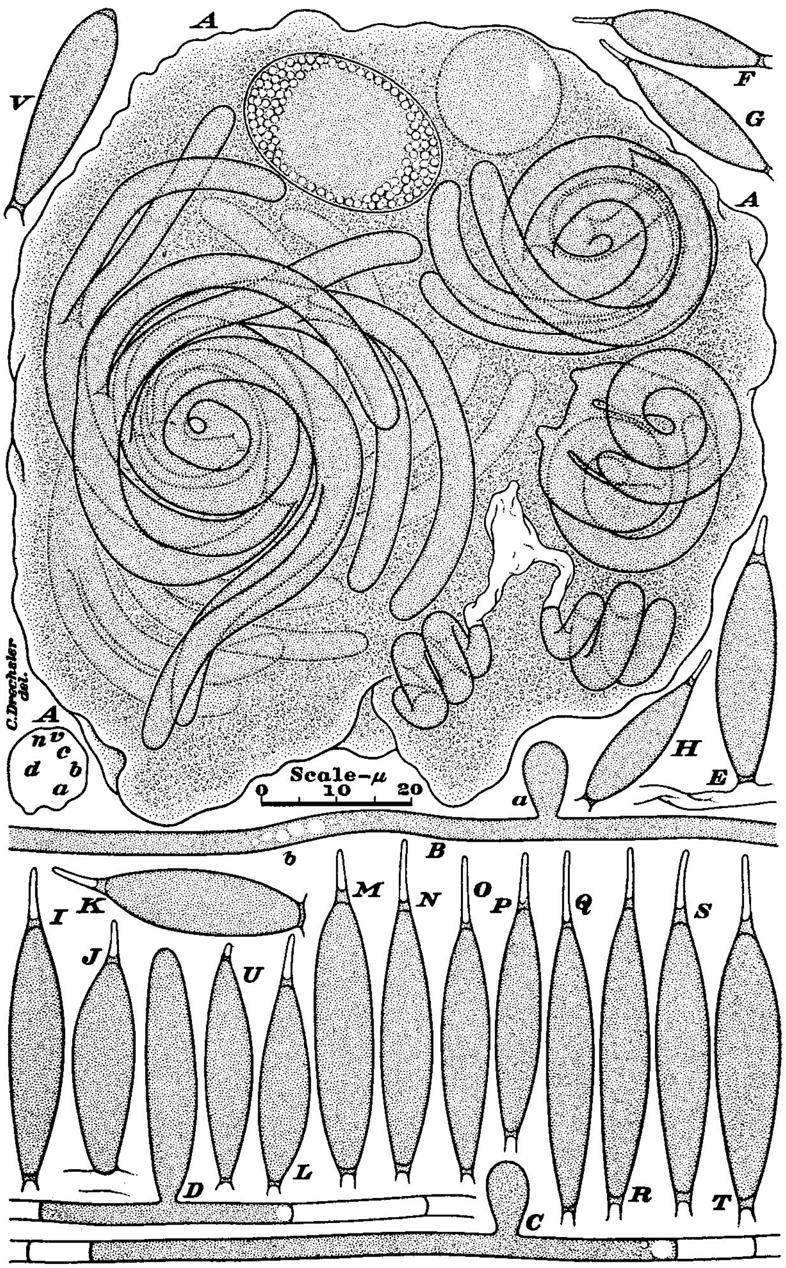

FIG. 4. *Endocochlus binarius.*

the thallus; the loss of contents usually becoming noticeable first in the distal parts of the coil (FIG. 6, *A, B*) and later in more proximal parts. Retaining walls are laid down at intervals in the progressive withdrawal of protoplasm (FIG. 6, *E*), much as in the other species of *Endocochlus,* as well as in most species of *Cochlonema.*

The reproductive hyphae destined to serve in the development of conidia push their way to the animal's integument without establishing any definite positional relationships to one another. On breaking through the pellicle they elongate radially from the dead animal until they extend procumbently over the surface of the culture for distances frequently of 2.5 to 3 mm. They usually show only rather gently curving deviations from their generally straightforward courses, and only small departures from their usual width of about 3 μ. After reaching their definitive length they soon put forth erect protuberances (FIG. 4, *B, a;* FIG. 5, *C, a-c*) often at intervals of 75 to 125 μ. Thereupon the hyphal contents near the middle of each interval become noticeably vacuolate (FIG. 4, *B, b*). As material is supplied for further growth of the protuberances the vacuolate portions are emptied and retaining walls are formed. Continued withdrawal of protoplasm soon leads to evacuation of an adjacent hyphal portion and deposition of another wall closer to the growing protuberance (FIG. 4, *C.* FIG. 5, *D, a-c; E*). With repetition of the process the living hyphal segment is further reduced (FIG. 4, *D.* FIG. 5, *F, a; G, a*), and finally, as a rule, the remaining hyphal contents migrate into the erect outgrowth, which then is delimited a little above the base by a thickish septum (FIG. 4, *E.* FIG. 5, *F, b; G, b*). During the later stages of its growth, the erect body usually extends upward a narrow apical prolongation, which is soon delimited at the base by a rather thick wall or somewhat irregular plug-like partition.

Although the erect conidium thus formed resembles that of *Endocochlus gigas* in the fusoid shape of the living cell, it is of generally greater dimensions throughout (FIG. 1, *B-Z.* FIG. 4, *F-V.* FIG. 5, *H, a-z; I, a-z; J, a-z*). It is distinguished more especially, however, by its narrow apical appendage, which as a rule is not only decidedly longer in actual measurement than the corresponding part in *E. gigas,* but is markedly longer also in comparison with the living cell; though in occasional specimens the appendage may be small

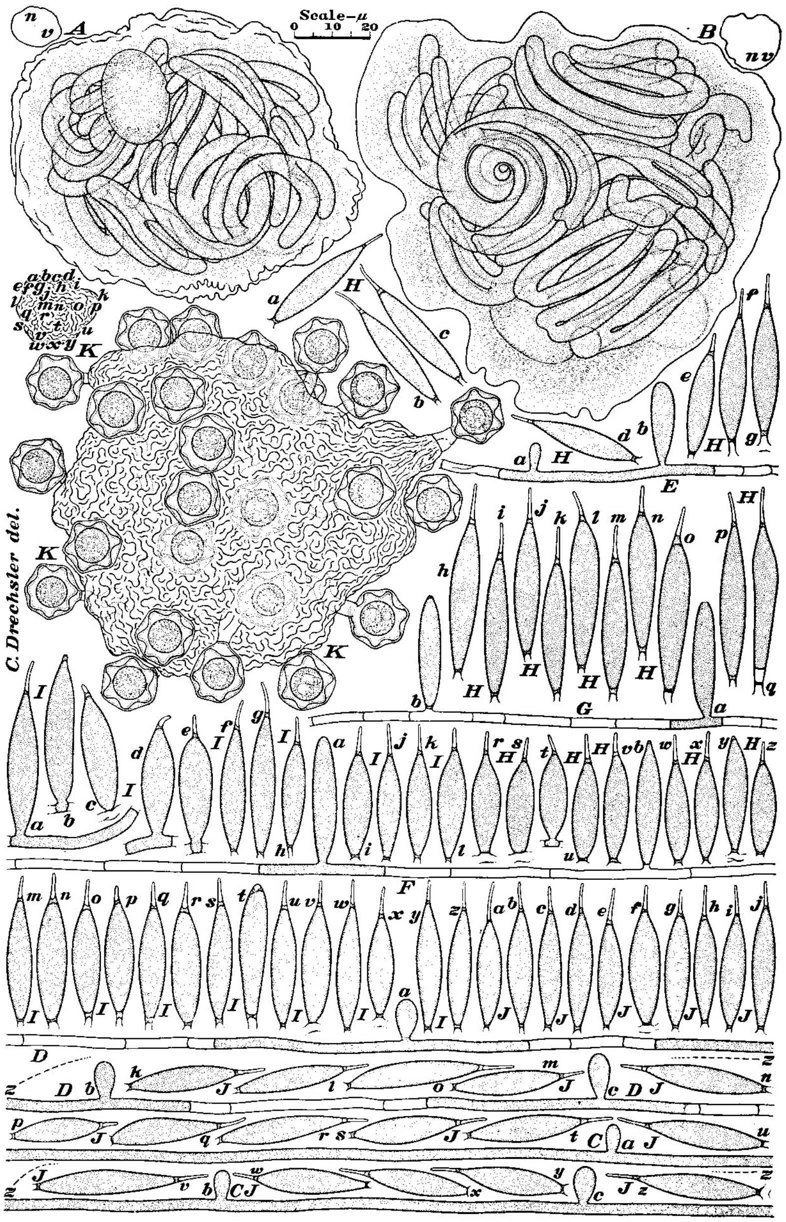

FIG. 5. *Endocochlus binarius.*

(FIG. 1, *X*; FIG. 4, *U*; FIG. 5, *I*, *c*, *t*), or may be present merely as a minute cap of solid wall material (FIG. 1, *V*, *W*. FIG. 4, *V*. FIG. 5, *F*, *b*; *G*, *b*; *H*, *y*; *I*, *b*), or in very imperfect specimens may be wholly absent (FIG. 1, *Z*). When the mature conidium becomes detached, it does not usually separate from the empty hypha flush with the lower side of its basal wall but is abjointed commonly at a distance of 0.5 to 2 μ or more rarely as much as 3 μ, from this wall; so that the spore carries at its base a curious membranous prolongation, a little like an appendage. This somewhat untidy manner of separation is not governed by chance, for the portion of hyphal membrane that accompanies the spore is always noticeably thicker than the hyphal envelope generally, and thus must have undergone earlier some special modification. In some instances where the basal septum was formed flush with the parent hypha, the membranous prolongation may include a cylindrical portion of the hyphal envelope (FIG. 1, *N*. *W*. FIG. 4, *J*. FIG. 5, *H*, *r*, *s*, *y*; *I*, *c*, *v*, *x*; *J*, *f*, *z*). Again, in occasional instances where because of incomplete transfer of protoplasmic contents the living cell of the detached spore includes a portion of the parent hypha (FIG. 1, *Y*, *Z*. FIG. 5, *H*, *t*; *I*, *a*, *b*, *d*, *e*), a short cylindrical portion of empty hyphal envelope is present at each of the two basal ends.

Germination has been observed taking place only in the conidia that have become affixed to the pellicle of a host animal. Nevertheless, in cultures where the fungus has been active on a large scale for a few days, the conidia strewn about on the substratum usually include many individuals with lateral outgrowths and membranous attachments of various shapes (FIG. 2, *B*-*M*). These modifications clearly derive from germinative development frustrated at different stages. In resisting infection from individual conidia of the fungus, *Amoeba papyracea* seems much more often successful than any other rhizopod I have hitherto seen undergoing attack by any zoöpagaceous parasite. In several observed instances the animal protruded a pseudopodium at the place of attack, thereby eventually confining the germ hypha in a small narrow-necked pouch. By persistent rotational movement of the animal the slender attachment was twisted off, and the pouch, consisting of a piece of pellicle and some protoplasm, was left behind adhering to the conidium (FIG. 2, *C*). The host animal appeared to carry out

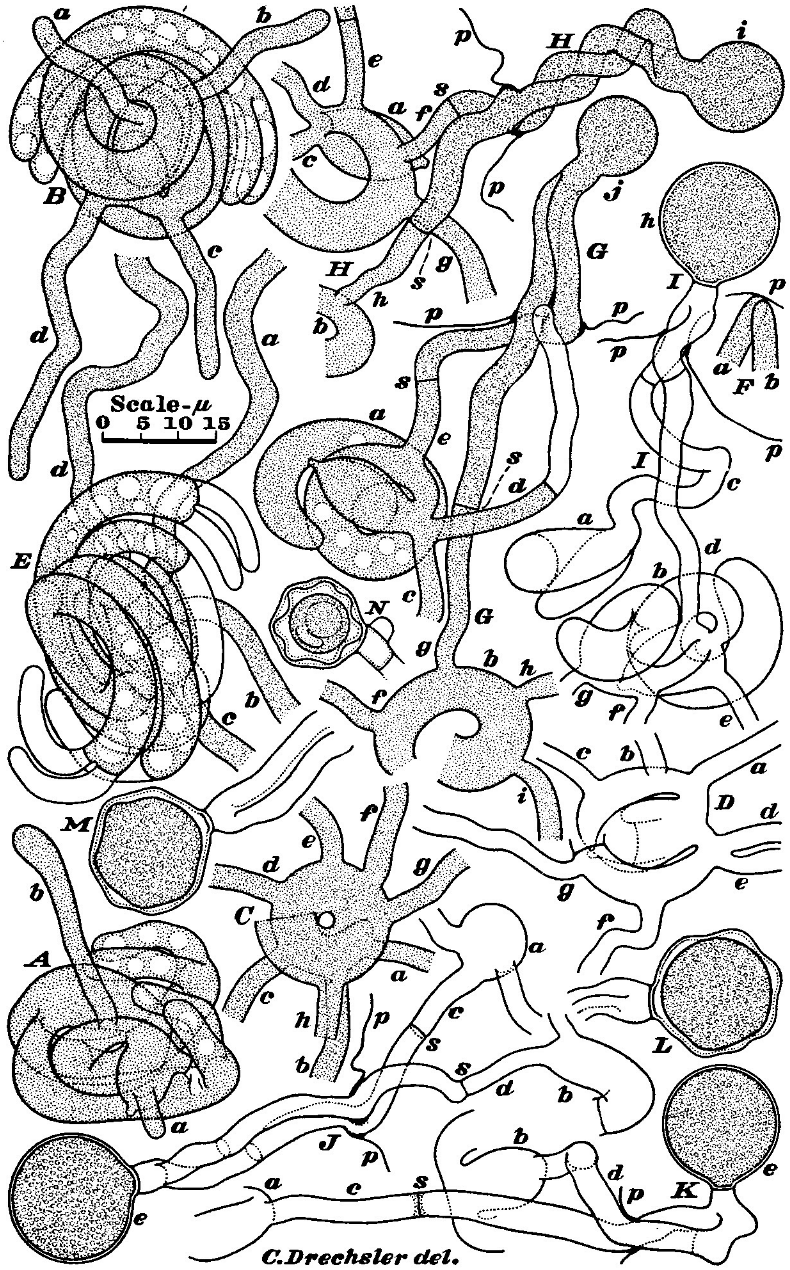

FIG. 6. *Endocochlus binarius.*

such defensive maneuvers repeatedly with different conidia, even when it was already infected with many growing thalli and thus was assuredly doomed. The conidia, on their part, were by no means rendered harmless by being sloughed off. If they had produced a long germ tube in their unsuccessful venture, the protoplasma in the tube was withdrawn backward into the spore envelope itself (FIG. 2, *E-G*), or into a short protruding stump (FIG. 2, *B, D, H*). If only appressoria had been formed, they were likewise evacuated when of large size (FIG. 2, *J*), but when relatively small (FIG. 2, *K-M*) were often left unchanged. Some conidia bore four or five frustrated germinative structures—appressoria and evacuated germ hyphae (FIG. 2, *F*)—thereby giving evidence of a corresponding number of unsuccessful attempts at infection.

The development of zygospores is initiated by reproductive hyphae of about the same width as those concerned in the formation of conidia. These hyphae make known their distinctive function by coming together in pairs inside the animal—the two members of a pair (FIG. 6, *F, a, b*) directing their growth in such wise as to bring their tips in contact with each other and at the same time with the inner surface of the animal's pellicle (FIG. 6, *F, p*). Pairing apparently never takes place between hyphae arising from the same vegetative thallus, single or binary; for in all instances where the difficulties of observation occasioned by the intertangling of fungus coils are not too troublesome, the two members of a pair are always traceable to separate thalli. Thus, in the reproductive apparatus shown in figure 6, *G,* where the two thalli *a* and *b* have each produced several reproductive hyphae, no pairing took place either between the three hyphae *c-e* arising from thallus *a,* or between the four hyphae *f-i* arising from thallus *b,* but the hypha *e* from thallus *a* was found paired with the hypha *g* from thallus *b.* Likewise in figure 6, *H,* showing portions of two thalli, *a* and *b,* no pairing could be made out between any of the five reproductive hyphae *c-g* arising from thallus *a,* but one of them, *f,* had paired with a hypha, *h,* coming from thallus *b.* Again in the reproductive apparatus shown in figure 6, *I,* the two empty thalli *a* and *b* are seen to have contributed the paired hyphae *c* and *d,* respectively, although the three additional hyphae *e-g* arising from thallus *b* have not paired with one another. Further, in the unit of sexual apparatus shown in figure 6, *J*, the empty thalli *a* and *b* have contributed the paired zygophoric hyphae *c* and *d*, respectively; while similarly in the unit of sexual apparatus illustrated in figure 6, *K*, the empty thallus *a* and the empty infective body *b*, separate from it, have given off the paired zygophoric hyphae *c* and *d*, respectively.

The paired zygophoric hyphae, on making apical contact with each other and also with the host animal's pellicle (FIG. 6, *G-K: p*), secrete at their tips some yellow adhesive material. Thus anchored securely to the pellicle, they break jointly through this envelope, and then elongate externally side by side for distances varying commonly from 5 to 35 μ before fusing at the tip. As a rule, and more especially where elongation takes place under the surface of a culture, the hyphae follow rather straightforward courses (FIG. 6, *G*). Where external elongation takes place on the surface of a culture the zygophoric hyphae in some instances wind spirally about one another, their direction of rotation then being indiscriminately either right-handed (FIG. 6, *H*) or left-handed, rather than consistently left-handed like the rotation in the thallodic coils.

When their elongation ceases the paired hyphae fuse apically and begin to bud forth a globose body (FIG. 6, *G, j; H, i*) directly at the place of union, or terminally on a short stout prolongation usually not more than 2 μ in length. Meanwhile a cross-wall (FIG. 6, *G, s; H, s; J, s; K, s*) proximally delimiting a gametangium makes its appearance in each of the paired hyphae and usually in a position well within the host pellicle. The globose body increases gradually in size as it receives protoplasmic material from the gametangia. When the gametangia have given all their contents, it usually has reached a definitive diameter of approximately 15 μ (FIG. 6, *I, h; J, e; K, e*) and then apparently becomes delimited at or near the base by a retaining wall. The protoplast of the subspherical zygosporangium thus set off soon shrinks away from the enveloping wall, which thereupon usually collapses slightly to present a somewhat wavy contour (FIG. 6, *L*). Later the protoplast takes on an angular shape (FIG. 6, *M*), preparatory evidently to the formation of a yellowish zygospore wall with a pronouncedly warty or stellate outline. Within this wall the originally granular contents round up into a spherical living cell (FIG. 3, *C-P;* FIG. 6, *N*). At maturity this cell seems to be constituted, as a rule, of an outer granular layer surrounding a more nearly homogeneous reserve globule and having imbedded in it a somewhat flattened refringent body. The internal organization of the resting zygospore here as in the several congeneric forms and in most other members of the Zoöpagaceae would seem to correspond to the unitary organization familiar in the resting oospores of many oomycetes, including most species of *Pythium* and all species of *Aphanomyces*.

As the individual zygospores are produced close to the host pellicle in numbers ranging usually from 10 to 25 (FIG. 5, *K, a-y*)—the greatest number noted was 37—and are of durable character, they arrest attention by their clustered arrangement for months after all vestiges of their protozoan hosts have vanished from sight. In some plate cultures many were observed being invaded and destroyed by a hyphomycete that developed mainly through parasitism on the oospores of *Pythium mamillatum*. Though a mycelial connection could not be traced the hyphomycete in question was most probably *Trinacrium subtile* Fres., since the distinctive conidia of that oospore parasite were present in some abundance. The same hyphomycete also parasitized many specimens of the testaceous rhizopod *Arcella vulgaris* Ehrenb. that were distributed on the surface of the agar, and further invaded numerous globose cysts which had been produced in the cultures by a member of the Myxobacteriaceae.

A term having reference to its predominantly binary vegetative development is deemed suitable as a specific name for the new fungus.

Endocochlus binarius sp. nov.

Corpus intromissum per tubulum germinationis nuciforme, plerumque 12–20 μ longum, 6–10 μ crassum, basi acutulum, apice primo rotundum, mox ex apice vulgo 2 (interdum 1 et rarius 3) hyphas assumentes pullulans, postea aliquando 1 vel 2 hyphas genitabiles (hyphas conidiiferas vel zygosporiferas) uspiam emittens; hyphis assumentibus incoloratis, prope basim 2–4.5 μ crassis, sursum leniter quandoque usque 8 μ latescentibus, usque 200 μ longis, in spiram semel vel bis vel ultra quam ter ad modum caulis Humuli lupuli cochleatim convolutis, nunc simplicibus nunc semel usque ter repetite bifurcis, animal debilitato vel moribundo prope originem ex latere convexo 1–8 hyphas genitabiles emittentibus. Hyphae conidiiferae per pelliculam animalis solitatim erumpentes, extra animal procumbentes et paene rectae, simplices vel parve ramosae, incoloratae, saepe 2.5–3 mm. longae, plerumque 2.5–3.3 μ crassae, primo continuae et protoplasmatis repletae, post auctum conidiorum inanes et septatae; conidiis inter se saepius 75–125 μ distantibus, incoloratis, erectis, post disjunctionem deorsum subter septo inferiore membrana circulari inani 1–3 μ longa praeditis, vulgo in cellula viventi et appendice vacua terminali consistentibus; cellula viventi ellipsoidea vel fusiformi, 20–45 μ longa, 5.7–9 μ crassa; appendice vacua 2–10 μ longa, deorsum plerumque 1–1.5 μ crassa, apice 0.6–0.8 μ crassa. Hyphae zygosporiferae 2–4.5 μ crassae, ambae ex aliis hyphis assumentibus oriundae, apice ad pelliculam animalis communiter inhaerentes, mox ex pellicula communiter erumpentes, communiter 5–35 μ in longitudine interdum spiraliter interdum recto crescentes, denique gametangiis terminalibus saepius 20–50 μ longis seclusis in apice conjungentes et zygosporangium ex junctione gignentes; zygosporangio globoso, plerumque 12–17 μ in diametro, membrana ejus in maturitate circum zygosporam laxe collapsa; zygospora flavida globosa, 11–15 μ crassa, membrana in maturitate valde verrucosa, cellulam viventem sphaeralem 8–10.5 μ crassam circumdante.

Amoebam papyraceam enecans habitat in foliis Quercus putrescentibus prope Greensboro, North Carolina.

Infective body formed on intruded germ tube usually elongated ellipsoidal, minutely protruding at the proximal end, rounded at the distal end, usually 12–20 μ long and 6–10 μ wide, from opposite positions on the distal end soon putting forth 2 (sometimes 1 and more rarely 3) assimilative hyphae, and later, on disablement or death of animal host, sometimes extending from indeterminate positions 1–2 reproductive (*i.e.*, conidiiferous or zygophoric) hyphae. Assimilative hyphae colorless, up to 200 μ long, near their attachment usually 2–4.5 μ wide, usually widening rather gradually to attain more distally sometimes a diameter of 8 μ, convolved in a helicoid spiral of 1–3.5 turns with left-handed rotation, simple or once-dichotomous or successively bifurcated 2–3 times; after disablement or death of host animal giving rise proximally from the convex side to reproductive hyphae in numbers ranging from 1 to 8. Conidiiferous hyphae erupting individually from the animal's pellicle to elongate procumbently in rather straightforward courses for distances frequently of 2.5–3 mm. at a width between 2.5 and 3.3 μ, simple or sparingly branched, at first continuous and filled with protoplasm, but becoming empty and septate in producing erect conidia at intervals frequently of 75–125 μ. Conidia colorless, consisting individually of an elongated ellipsoidal or spindle-shaped living cell, 20–45 μ long and 5.7–9 μ wide, surmounted usually by an empty tapering appendage 2–10 μ long, 1–1.5 μ wide proximally, and tapering to a width of 0.6–0.8 μ near the tip; the individual spore usually becoming detached a short distance below its basal septum, and thus bearing proximally an empty collar-like membranous prolongation 1–3 μ long. Zygophoric hyphae 2–4.5 μ wide, each pair arising from separate assimilative structures, the two usually making close contact at their apices before breaking jointly through the host pellicle to elongate together outside 5–35 μ usually in a straightforward course but sometimes winding spirally about one another, then (terminal gametangia often 20–50 μ long having been delimited) fusing at the tip and budding forth a zygosporangium from the place of union. Zygosporangium globose, usually 12–17 μ in diameter, its wall at maturity collapsing loosely about the zygospore. Zygospore subspherical, 11–15 μ in diameter, slightly yellowish, its wall at maturity presenting a somewhat stellate profile around a spherical protoplast 8–10.5 μ in diameter.

Destroying *Amoeba papyracea* it occurs in decaying Quercus leaves near Greensboro, North Carolina.

DIVISION OF FRUIT AND VEGETABLE CROPS AND DISEASES,
PLANT INDUSTRY STATION,
BELTSVILLE, MARYLAND

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EXPLANATION OF FIGURES

FIG. 1. *Endocochlus binarius,* drawn to a uniform magnification with the aid of a camera lucida; × 1000 throughout. *A,* Specimen of *Amoeba papyracea* in active condition though under multiple attack by the fungus, with

the fungus in various stages of development: *a*, adhering conidium with a funnel-shaped germinative outgrowth that has penetrated the animal's pellicle and is forming terminally an infective body in the host protoplasm; *b*, adhering conidial envelope that has been emptied by movement of its contents through the tapering germ tube into the terminal infective body, which now is fully formed and delimited at its base by a retaining wall; *c*, newly detached infective body; *d*, *e*, two infective bodies, each of which has begun to grow out distally into a single thallodic coil; *f*, an infective body that has grown out distally into a single thallodic coil of two turns; *g*, infective body that is budding out in opposite positions at its distal end, to begin the development of two thallodic coils; *h*, similar infective body whose two distal outgrowths are somewhat longer and thus show in the orientation of their expanded tips the left-handed rotation characteristic of the vegetative stage of the fungus; *i*, infective body with two regularly convolved thallodic coils, each coil consisting of one and one-half turns; *j*, infective body with two less regularly convolved thallodic coils, each consisting of approximately one and one-fourth turns; *k*, empty infective body that has produced two regularly convolved thallodic coils, each of approximately two turns and each delimited proximally by a retaining wall; *l*, infective body with two regularly convolved thallodic coils shown endwise, each coil consisting of about one and one-half turns; *m*, infective body with two regularly convolved thallodic coils, each of which is bifurcated about one and one-half turns from its origin; *n*, nucleus of animal host; *o*, large infective body that has put forth three thallodic outgrowths, each disposed in a left-handed coil of about one-half turn; *v*, contractile vacuole of animal host; *w*, encysted specimen of *Euglypha levis* ingested by animal host. *B–U*, Conidia of usual make-up, showing ordinary variations in size and shape, and in length of empty beak. *V*, *W*, Conidia with short apical beaks that apparently are not empty. *X*, Conidium with small empty apical beak. *Y*, Conidium including at the base a portion of the parent hypha. *Z*, Conidium lacking an apical beak, and at the base including a portion of the parent hypha.

FIG. 2. *Endocochlus binarius*, drawn to a uniform magnification with the aid of a camera lucida; × 1000 throughout. *A*, Specimen of *Amoeba papyracea* still actively motile though under multiple attack by the fungus: *a*, infective body that has grown out distally to form a young thallodic coil of one-half turn; *b*, infective body with two regularly convolved thallodic coils, each consisting of approximately a three-fourth turn; *c*, infective body with two somewhat irregularly convolved thallodic coils, each comprising approximately one turn; *d*, infective body (viewed from the proximal end) with two thallodic coils, each composed of one turn; *e*, infective body with two regularly convolved thallodic coils, each comprising slightly more than one turn; *f*, infective body (viewed from the distal end) bearing two regularly convolved thallodic coils, each of slightly more than one turn; *g*, infective body (likewise viewed from distal end) bearing two regularly convolved thallodic coils, each comprising about one and one-half turns; *h*, empty collapsed membranous envelope of an infective body, to which are attached two regularly convolved thallodic coils, each delimited proximally by a retaining wall and comprising two turns; *i*, infective body that has grown out into a single thallodic coil, which bifurcated one and three-fourth turns from its

origin; *j, k,* infective bodies (in oblique view), each with two thallodic coils, one of them being simple, the other one being bifurcated about one-half turn from its origin; *n,* nucleus of animal host; *v,* contractile vacuole of host; *w,* ingested specimen of *Euglypha levis. B–M,* Conidia with various lateral modifications ranging from 1 to 5 in number, each resulting from frustrated infective germination: in *C* the broad adhesive appressorium has attached to it a portion of pellicle and protoplasm torn from an animal in its successful escape; in *D* the distally evacuated germ tube is shown encased in a remnant of protoplasm from an animal that escaped infection after deep penetration by the fungus.

FIG. 3. *Endocochlus binarius,* drawn to a uniform magnification with the aid of a camera lucida; × 1000 throughout. *A,* Specimen of *Amoeba papyracea* still in motile condition though under multiple attack by the fungus: *a,* infective body that has grown out distally into a single thallodic prolongation, which began coiling later than is usual; *b, c,* infective bodies that have each grown out into a single thallodic coil of a three-fourth turn; *d, e,* infective bodies, each of which has grown out into an irregularly convolved thallodic coil of one and one-half turns; *f, g,* infective bodies, each of which has grown out into a single thallodic coil that is bifurcating after describing one and three-fourth turns; *h,* infective body with two thallodic coils, each comprising a single turn; *i,* infective body with two thallodic coils of a single turn, the coil attached on the left showing departure from the usual in having taken a course on the same side of the infective body as the coil attached on the right; *j,* single coiled bifurcate thallus comprising two and one-half successive turns, which is not attached to any visible infective body; *k,* infective body bearing two thallodic coils, only one of which is shown with its two and one-half successive turns and its two bifurcations; *n,* nucleus of animal host; *v,* contractile vacuole of animal. *B,* Infective body with two thallodic coils, each of them once bifurcate and each consisting of two and one-half successive turns: *a,* the complete assimilative structure, with all parts in place; *b,* the infective body with the one thallodic coil underneath it; *c,* the infective body with a proximal portion of each thallodic coil; *d,* the infective body with the one thallodic coil overlying it. *C, D,* Portions of empty paired zygophoric hyphae whereon are borne globose zygosporangia, each containing a zygospore somewhat immature in the organization of its protoplast. *E–P,* Zygosporangia, each containing a zygospore having a prominently warty envelope and a subspherical protoplast of mature structure.

FIG. 4. *Endocochlus binarius,* drawn to a uniform magnification with the aid of a camera lucida; × 1000 throughout. *A,* Specimen of *Amoeba papyracea* still in active condition though under multiple attack by the fungus: *a,* empty membranous envelope of infective body bearing two regularly convolved thalli, each comprising two and one-half turns and each delimited proximally by a retaining wall; *b,* infective body bearing two regularly convolved unbranched thallodic coils, each consisting of one and three-fourth turns; *c,* thallodic coil, comprising two and one-half successive turns and showing two bifurcations, which no longer is attached to any visible infective body; *d,* well developed thallodic coil, convolved in three to three and one-half successive turns and showing three successive bifurcations, which lies over its companion whereof only the eight terminations directly exposed

to view are shown, their contours being drawn with stippled lines; *n*, nucleus of animal host; *v*, contractile vacuole of animal. *B*, Portion of a continuous prostrate conidiiferous hypha showing a conidium, *a*, in early stage of development, and a cluster of vacuoles, *b*, resulting from initial loss of hyphal contents. *C*, Portion of prostrate conidiiferous hypha showing a young conidium, and several partitions formed on progressive evacuation of hyphal parts. *D*, Portion of prostrate conidiiferous hypha showing a conidium in more advanced stage of development. *E*, Portion of empty prostrate hypha with a fully developed conidium. *F–U*, Fully developed conidia showing usual variations in size and shape of both the living cell and the empty apical beak. *V*, Conidium in which the apical beak is reduced to a thickened cap.

FIG. 5. *Endocochlus binarius*, drawn to a uniform magnification with the aid of a camera lucida; × 500 throughout. *A, B*, Two specimens of *Amoeba papyracea* no longer capable of locomotion owing to advanced infection of each by approximately ten thalli variously intertangled and massed in a confused clew; the two animals, despite marked degeneration of their nuclei, *n*, and reduction of their protoplasm to about one-tenth of the normal quantity, still showing life in continued operation of their contractile vacuoles, *v*. *C*, Portion of continuous conidiiferous hypha showing three conidia, *a–c*, in early stage of development; owing to lack of space the hyphal portion is shown in two parts connecting at the point *z*. *D*, Portion of conidiiferous hypha with empty intervals that were evacuated and partitioned owing to progressive movement of contents into the three growing conidia *a–c*; the hyphal portion being shown, from lack of space, in two parts connecting at the point *z*. *E*, Short portion of conidiiferous hypha on which two conidia, *a* and *b*, are being formed. *F, G*, Largely evacuated portions of conidiiferous hypha, each showing a conidium, *a*, in advanced stage of development, and a fully developed conidium, *b*. *H–J*, Random assortment of conidia, *a–z*, showing variations in size and shape of the living cell and of the apical beak, as well as in the length of the basal membranous prolongation; a few examples (*H, t; I, a, b, d, e*) showing variable extension of protoplasm into the parent hypha. *K*, Wrinkled collapsed pellicle of a large specimen of *Amoeba papyracea* surrounded by twenty-five zygosporangia of the parasite, *a–y*, each containing a prominently warty zygospore with a spherical protoplast in mature resting condition.

FIG. 6. *Endocochlus binarius*, drawn to a uniform magnification with the aid of a camera lucida; × 1000 throughout. *A*, Infective body with a twice bifurcated thallodic coil of two successive turns; one reproductive hypha, *a*, is growing out directly from the infective body, and another, *b*, from the proximal portion of the coil. *B*, Infective body with two thallodic coils, each comprising one and three-fourth turns and bifurcating once; two reproductive hyphae, *a* and *b*, are growing out from the infective body, while two others, *c* and *d*, are being extended from the basal portions of the coils. *C*, Proximal portion of a thallodic coil from which eight reproductive hyphae, *a–h*, have been extended; the infective body from which the coil originated is no longer visible. *D*, Empty membranous envelope of an infective body and of proximal portions of two thallodic coils; three empty reproductive hyphae, *a–c*, are shown arising from one coil, and four similar hyphae, *d–g*,

are shown arising from the other. *E*, Branched helicoid thallus with six terminal elements, each of which is partly or wholly emptied and provided with a retaining wall; below these walls the contents show pronounced vacuolization; four reproductive hyphae, *a–d*, are given off from the proximal turn. *F*, Tips of two zygophoric hyphae, *a* and *b*, making contact on the inner side of the host pellicle, *p*. *G*, Two helicoid thalli, *a* and *b*, the former having put forth three reproductive hyphae, *c–e*, the latter having put forth four such hyphae, *f–i*; after the hyphae *e* and *g* had paired by tip-to-tip contact on the inner surface of the host pellicle, *p*, they grew through the pellicle side by side for a distance of 20 μ and then fused apically to begin development of the partly grown zygosporangium, *j*; a septum, *s*, had in the meantime been formed in each hypha to delimit the paired gametangia; the hypha *d* is present as a frustrated supernumerary zygophore. *H*, Two helicoid thalli, *a* and *b*, that have put forth the reproductive hyphae *c–h*; the hypha *f* (from thallus *a*) having paired with hypha *h* (from thallus *b*) by apical contact on the inner surface of the host pellicle, *p*, the two broke jointly through the pellicle and elongated outside for a distance of 25 μ while winding about one another before they fused apically to give rise to the globose zygosporangium *i*; a septum, *s*, having meanwhile been formed in each zygophoric hypha to delimit the paired gametangia. *I*, Two empty helicoid thalli, *a* and *b*, from which were put forth the reproductive hyphae *c–g*; after the hyphae *c* and *d* (originating from thalli *a* and *b*, respectively) had paired by making contact on the inner surface of the host pellicle, *p*, the two erupted jointly to elongate externally for a distance of 5 μ, and then fused apically to form the zygosporangium *h*, now fully grown and delimited at the base. *J*, Parts of two empty thalli, *a* and *b*, from which were extended the zygophoric hyphae *c* and *d*, respectively; the two hyphae, after becoming paired by adhering together apically on the inner side of the host pellicle, *p*, having erupted and grown externally side by side for a distance of 25 μ, then having fused apically to form the zygosporangium *e*, now fully grown and delimited at the base; *s*, septa delimiting the paired gametangia. *K*, Portion of empty thallus, *a*, and an empty infective body, *b*, from which were extended the zygophoric hyphae *c* and *d*, respectively; these hyphae, after becoming paired through mutual adhesion on the inner side of the host pellicle, *p*, having erupted together and grown externally side by side for a distance of 15 μ, then having fused apically to form the zygosporangium, now fully grown and delimited at the base; *s*, septum delimiting the gametangium supplied by hypha *c*. *L, M*, Two zygosporangia whose protoplasts have shrunken away from the slightly collapsed envelopes to form young zygospores. *N*, Slightly collapsed zygosporangial envelope surrounding a mature zygospore with boldly verrucose wall and subspherical protoplast.